

A NEW GENUS AND SPECIES OF STYGOBIONTIC
DRYOPID BEETLE, *STYGOPARNUS COMALENSIS*
(COLEOPTERA: DRYOPIDAE),
FROM COMAL SPRINGS, TEXAS

Cheryl B. Barr and Paul J. Spangler

Abstract.—A stygobiontic new genus and species, *Stygoparnus comalensis*, from Comal Springs, Texas, is described and compared with the dryopid genus *Helichus*. Distinctive characters of the adult and larva are illustrated with pen and ink drawings and scanning electron micrographs. This new taxon is the first member of the family Dryopidae reported from subterranean waters.

Most aquatic entomologists agree that our present aquatic insect fauna evolved from terrestrial taxa (Ross 1965, Wootton 1972, Resh & Solem 1984). Among the 22 families of aquatic and semiaquatic beetles known from the Western Hemisphere, there are two, Torridincolidae and Noteridae, that are known to be aquatic in all stages. In some of the other families, the adults are terrestrial and their larvae aquatic, while in others the reverse is true. There are taxa with stages that are terrestrial, semiaquatic, or aquatic in families like the Hydrophilidae. The hydrophilids are sometimes cited as examples of taxa derived from terrestrial progenitors (Crowson 1960, 1981; Miller 1963).

Evidence is accumulating that Western Hemisphere members of the family Dryopidae also show an evolutionary sequence similar to that of the hydrophilid beetles. Previously, the only known aquatic dryopids were the adults of the genera *Elmoparnus* Sharp, 1882, *Helichus* Erichson, 1847, and *Postelichus* Nelson, 1989; and the known larvae of the three genera were reported to be terrestrial (Doyen & Ulrich 1978, Spangler 1981, Ulrich 1986). Adults of the dryopid genera *Guaranius* Spangler, 1991, *Holcodryops* Spangler, 1987, *Protoparnus* Sharp, 1883, *Quadryops* Perkins & Spangler, 1985, *Sostea* Pascoe, 1860, and

Sosteamorphus Hinton, 1936b, are known only from terrestrial habitats. The larvae of these genera are unknown but presumed to be terrestrial. Adults of *Dryops* Olivier, 1791, *Pelonomus* Erichson, 1847, and *Onopelmus* Spangler, 1980, are known riparian taxa usually found on rocks and vegetation above water at the air-water interface. Larvae of *Dryops* and *Pelonomus* are reported to be terrestrial (Hinton 1936a, 1955; Chandler 1956; Berjon 1964; Brown 1991), and those of *Onopelmus* are presumed to be terrestrial (Spangler 1980).

The world fauna and characteristics of aquatic stygobiontic beetles were reviewed by Spangler in 1986. He reported 16 species in the families Dytiscidae, Elmidae, Hydrophilidae, and Noteridae. *Stygoparnus comalensis* is the world's first known stygobiontic member of the Dryopidae.

Habitat and Fauna

The Edwards Aquifer (Balcones Fault Zone) of central Texas is a vast underground storehouse of water fed by streams from the south and west. Water is "captured" as recharge by the aquifer when surface streams cut across the highly porous and fractured Edwards Limestone formation. The water then emerges as artesian springs along the Balcones Escarpment. The aquifer is be-

lieved to contain extensive water-filled caverns and caves (Pettit & George 1956, Klemt et al. 1979).

The Comal Springs complex in New Braunfels is the largest in Texas and discharges a mean historic flow of about 300 cubic feet per second (cfs) (8.31 cubic meters per second [cms]) (Ogden et al. 1986). The springs emerge at an elevation of 190 m from the Comal Springs fault along the base of a steep bluff that marks the edge of the Balcones Escarpment. Most of the water enters the aquifer as much as 100 km to the west; faulting has hydrologically isolated Comal Springs from any large sources of local recharge (Brune 1981, Pearson et al. 1975, Rothermel & Ogden 1987). This water may flow through the aquifer at depths as great as 150 m before surfacing at the springs (Brune 1981). Four main spring orifices, Comal 1–4 (j, k, l, b; Brune 1981) have been identified and hydrologically monitored by the Edwards Aquifer Research and Data Center (EARDC). Several minor outlets are also present. The Comal 1, 2, and 3 orifices are located in city-owned Landa Park. The spring runs, confined by concrete and rock walls, flow into Landa Park Lake, which is the headwaters of the Comal River. Increasing withdrawal of ground water has caused decreasing spring flow in recent years. Modeling has predicted that Comal Springs, as well as nearby Hueco and San Marcos springs, will permanently go dry as early as the year 2020 (Klemt et al. 1979).

The Edwards Aquifer is one of the most diverse subterranean aquatic ecosystems in the world in terms of richness of troglobitic species (Longley 1981, 1986). Forty-two species and/or subspecies of stygobiotic animals have previously been described from the artesian zone (Hershler & Longley 1986). Of these, the only insect is the stygobiotic dytiscid beetle *Haideoporus texanus* Young & Longley, 1976, from a well in San Marcos, the larva of which was described by Longley and Spangler (1977).

Heterelmis comalensis Bosse, Tuff, & Brown, 1988, an elmid beetle from Comal Springs, is believed to be endemic but not stygobiotic.

The senior author visited Comal Springs on four separate occasions. All four major orifices and two smaller outlets near Comal 4 were sampled (Fig. 1), but *Stygoparnus comalensis* was found only at Comal 2 springhead and associated run (Fig. 2). Nearby Hueco and San Marcos springs were also sampled without success. Likewise, other collectors have found *S. comalensis* only in Comal 2 and run. The adult beetles were all taken in the upper third to fourth of the spring run (Fig. 2); most specimens were collected from the headwater outlets (Figs. 3, 4) or from outlets beneath either bank (Fig. 5), but a few were taken from mid-stream. The larvae were collected from some of the same outlets; but because they are thought to be terrestrial, the microhabitat is presumed to be the ceilings of the orifices. Water covered only part of the openings and soil, roots, and debris were exposed above the water line (Fig. 5); some of the material was dislodged while sampling.

The substrate of the spring outlets and run consists of coarse sand and angular rock fragments. When sampled by the senior author, the water was clear and ranged from about 5–31 cm deep. As monitored from September 1982 to July 1984 by the EARDC, water parameter ranges included the following: daily discharge, 1.3–8.2 cfs; water temperature, 22.6–24.6°C; dissolved oxygen, 3.1–5.5 ppm; and pH, 6.88–8.81 (Ogden et al. 1985a, 1985b).

Stygoparnus, new genus

Type species.—*Stygoparnus comalensis*, new species.

Diagnosis.—*Stygoparnus* may be distinguished readily from all other described dryopid genera by its vestigial eyes and 8-segmented antennae.

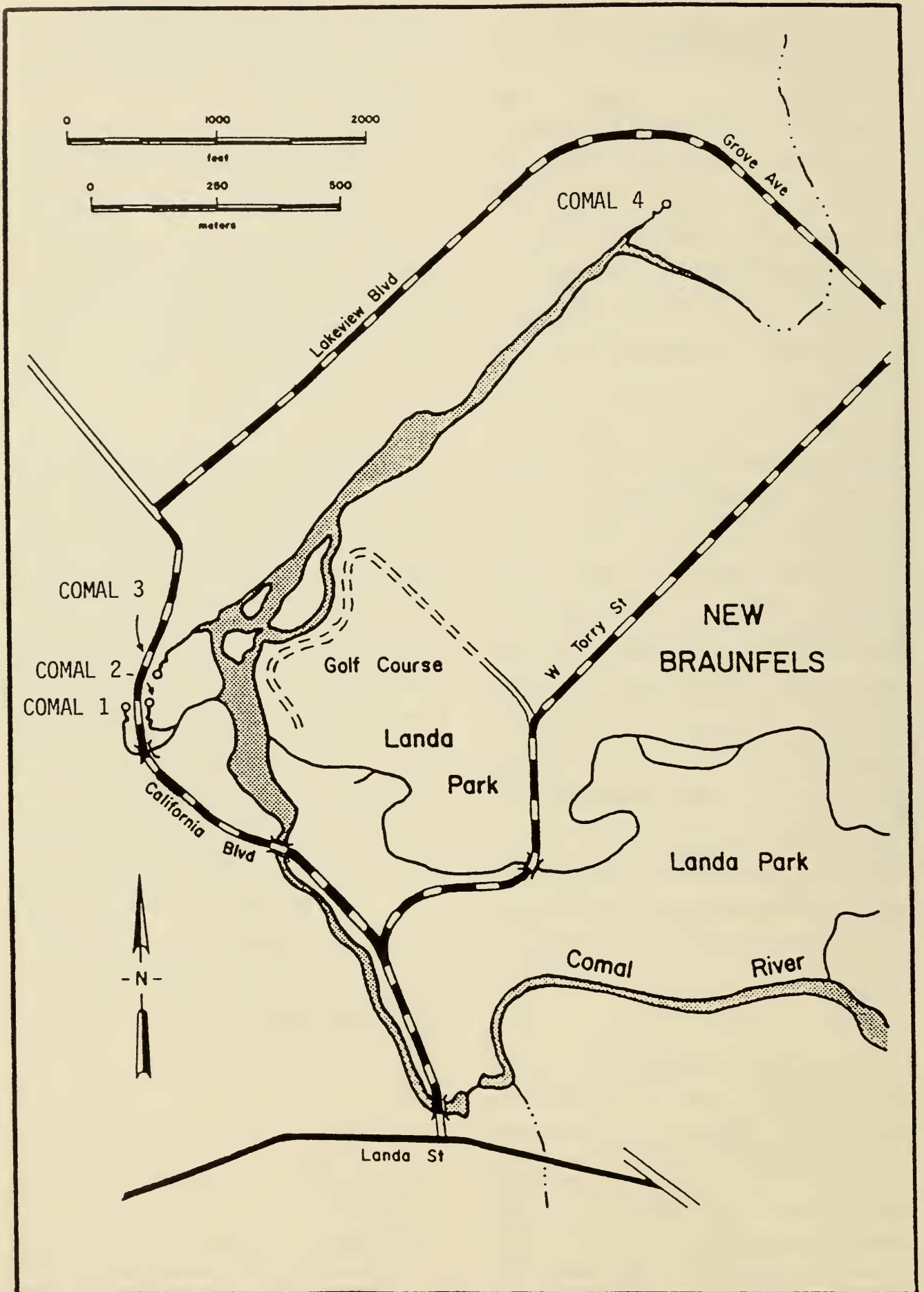
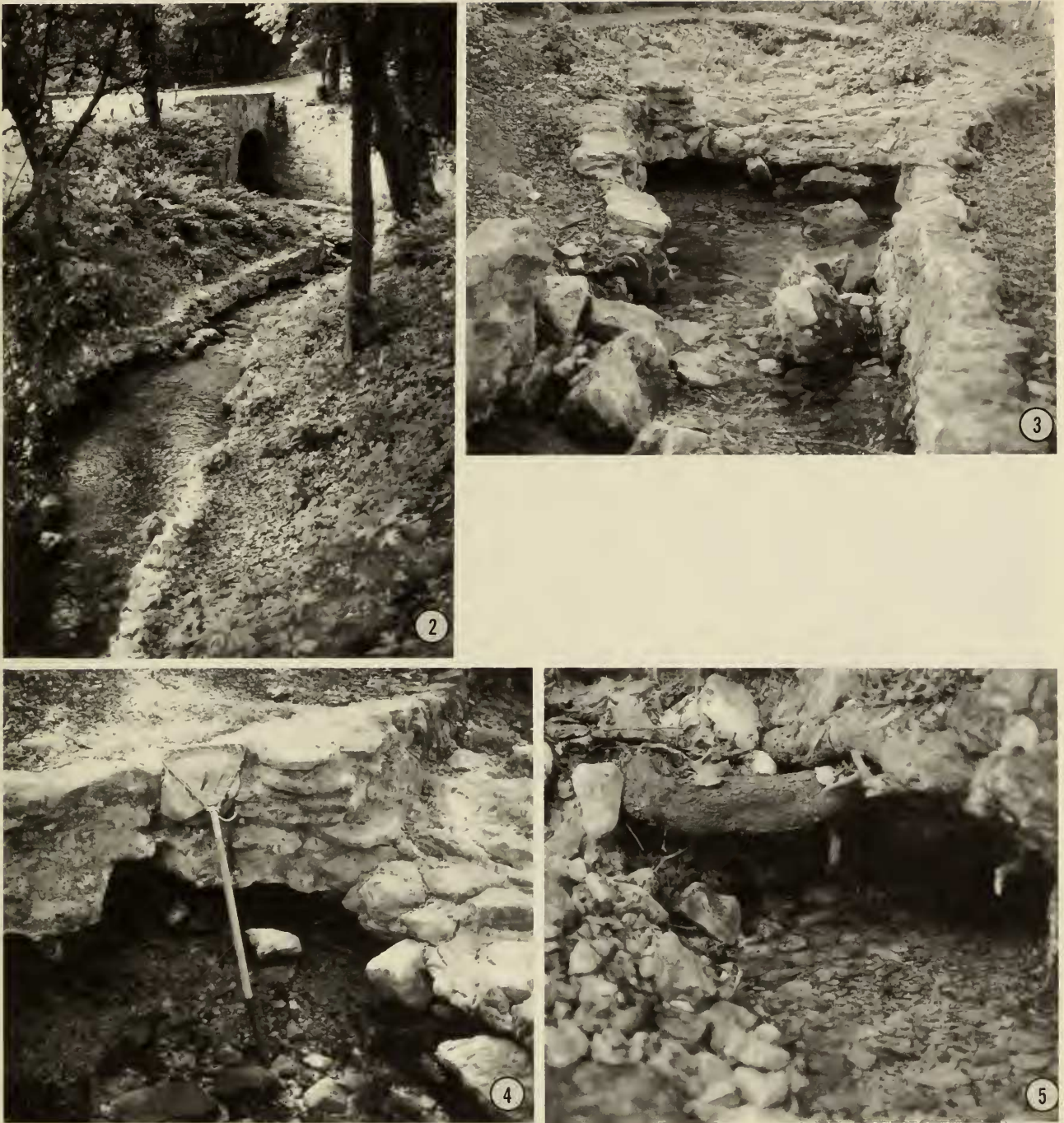


Fig. 1. Location of sampled orifices of Comal Springs, New Braunfels, Texas (from Ogden et al. 1985a).



Figs. 2-5. *Stygoparnus comalensis*, new genus, new species, biotope; Comal 2 springhead and run, Comal Springs, New Braunfels, Texas (photo by W. D. Shepard): 2, springhead and run; 3, springhead; 4, springhead, with aquatic net for scale; 5, spring outlet with ceiling exposed to air.

Adult (Figs. 6, 8-10).—Body form oblong, slender; depressed dorsally, convex ventrally. Cuticle thin, translucent. Indumentum of inconspicuous, fine, recumbent setae and plastron setae. Head retractile, slightly depressed dorsally. Eyes vestigial, reduced to several minute ocellus-like structures (Figs. 11, 17-19). Antenna, 8 segmented (Fig. 7); fitting into shallow acetab-

ula; basal segment small, subtriangular; segment 2 large, trapezoidal, shield-like, covering and enclosing pectinate segments 3-8. Clypeus expanded laterally beneath antennal insertions. Maxillary palpus, 4 segmented; apical segment cylindrical, about 2 times as long as combined length of basal 3 segments. Apicolateral sensory pit on last segment of maxillary palpus ovoid, not

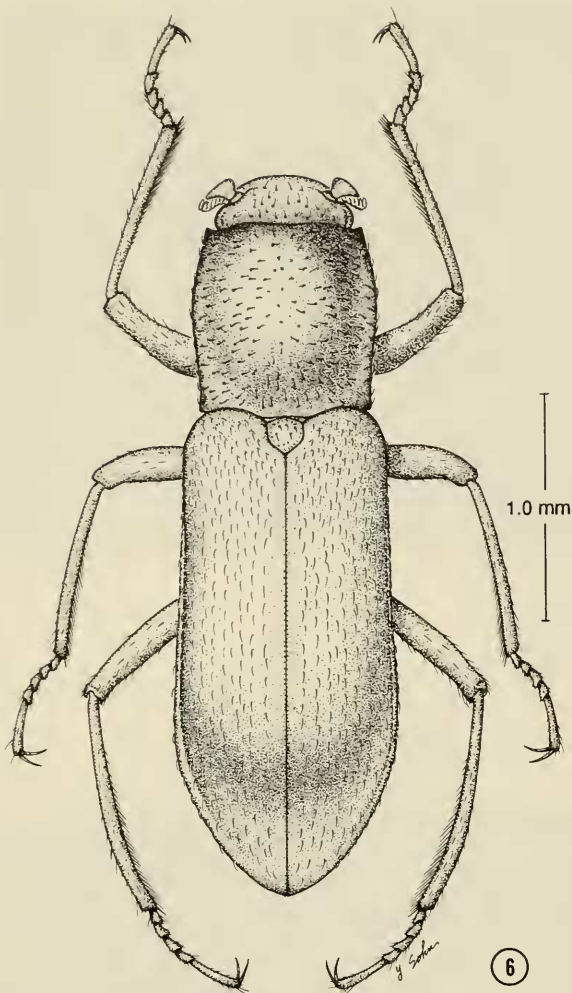


Fig. 6. *Stygoparnus comalensis*, new genus, new species, male: habitus, dorsal view.

deeply invaginated (Figs. 12–14). Labial palpus, 3 segmented; apical segment subovoid, slightly longer than combined length of basal 2 segments and broad, about 2 times as wide as penultimate segment (Fig. 18). Pronotum rectangular and slightly depressed, without sulci or carinae; anterior margin subtruncate; lateral margins smooth; prescutellar emargination well developed (Fig. 17). Scutellum large. Elytra wider at base than base of pronotum, depressed, without prominent punctures or striae; each elytron with shallow lateral groove extending from humerus to apex. Metathoracic wings vestigial, between $\frac{1}{3}$ to $\frac{1}{2}$ length of elytra (Figs. 20, 21). Prosternum long in front of procoxae. Prosternal process broad; apex angulate, slightly recurved, fitting into deep mesosternal fovea. Suture between mesosternum and metasternum indistinct. Meta-

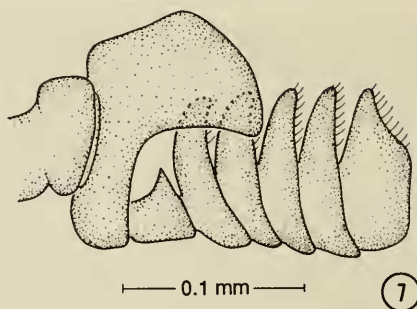
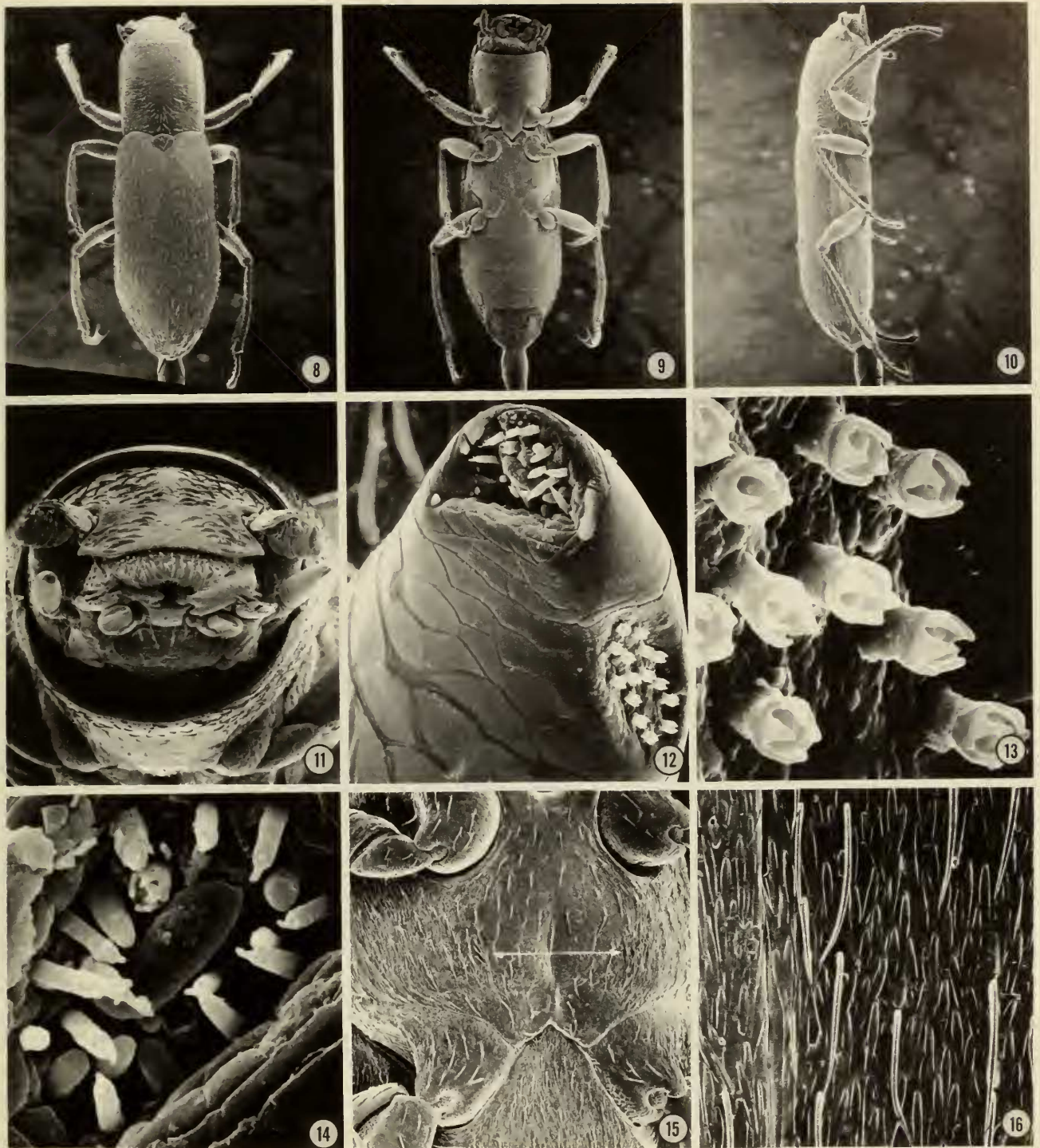


Fig. 7. *Stygoparnus comalensis*, new genus, new species, male: antenna, oblique view (to show segments).

sternum with discrimen not extending onto intercoxal process, crossed by short transverse sulcus just anterior to metacoxae (Fig. 15). Each pair of coxae about equally transversely separated. Metacoxae deeply dividing abdominal sternum 1. Legs long, slender; middle leg shortest, hind leg longest. Femora moderately expanded, shorter than tibiae. Tarsal formula, 5-5-5. Last tarsal segment about as long as combined length of 4 preceding segments. Tarsal claws rather slender, without teeth. Abdomen of 5 visible segments; sterna decreasing in length toward apex except apical sternum as long as combined length of 2 preceding sterna. Apical sternum without plastron setae.

Etymology.—*Stygoparnus*, from the Latin *Stygius* (of the Styx, a river in the Nether World); plus *parnus*, a generic name coined by Fabricius for a dryopid genus now a junior synonym of *Dryops* Olivier; gender masculine.

Larval diagnosis (late instar; by association).—Cylindrical, elateriform (Fig. 30). Light yellow brown. Head partially retracted into prothorax; hypognathous. Epicranial and frontal sutures complete (Figs. 31, 32). Antennae, 3 segmented (Figs. 24, 35). Stemmata absent. Mandible stout, with 3 blunt apical teeth; without mola or prosthema (Figs. 33, 34). Maxilla fused with labium; maxillary palpus, 4 segmented (Fig. 25); galea and lacinia separate, each with apical spines (Figs. 36, 37). Labium with palpiger and 2-segmented palpus. Prothorax as long as combined length of mesotho-

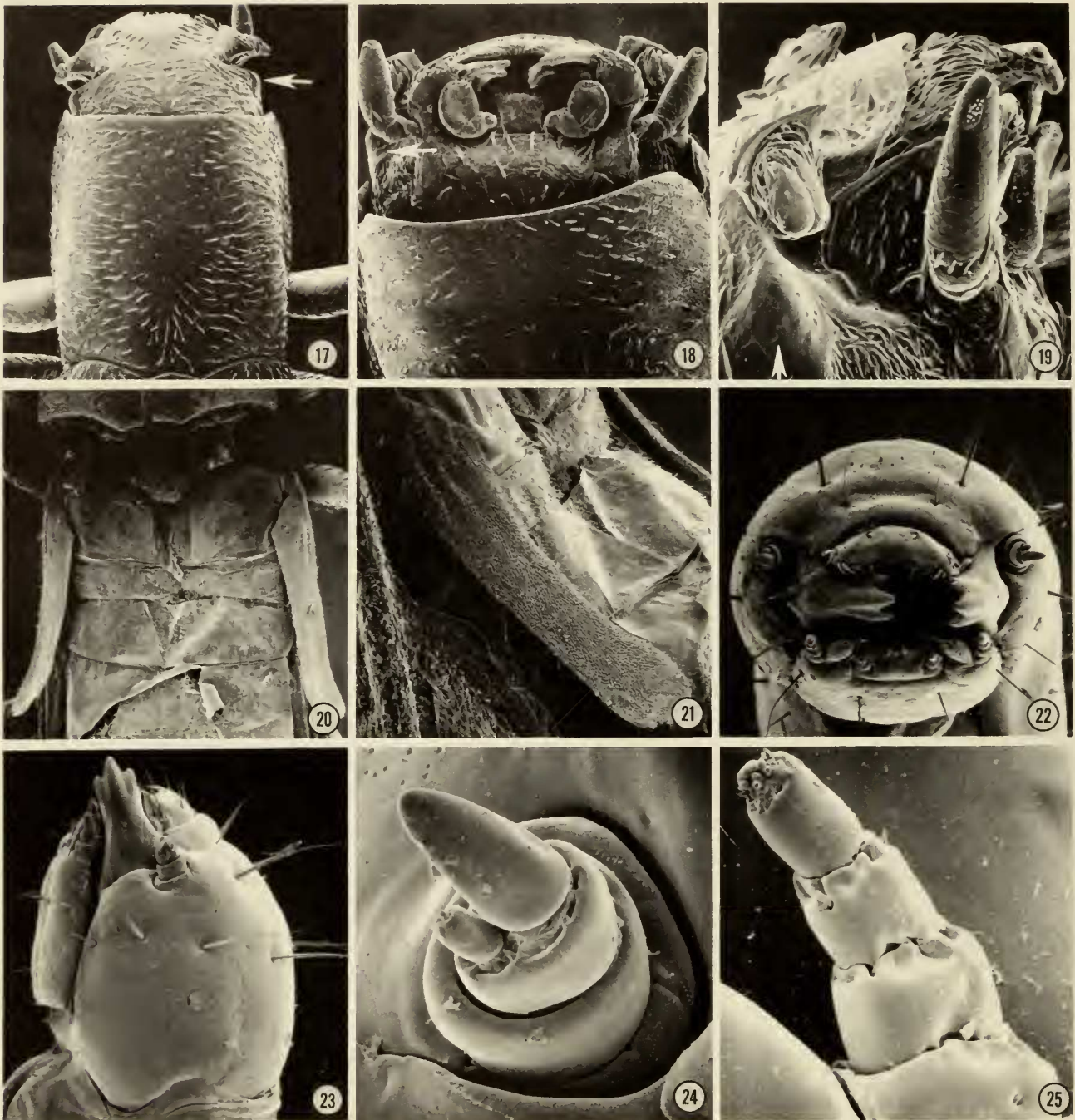


Figs. 8–16. *Stygoparnus comalensis*, new genus, new species, male: 8, habitus, dorsal view, $\times 30$; 9, habitus, ventral view, $\times 30$; 10, habitus, lateral view, $\times 30$; 11, head and mouthparts, adoral view, $\times 120$; 12, maxillary palpus, sensilla on apex of last segment, $\times 1700$; 13, maxillary palpus, sensilla, and apicolateral pit, $\times 10,000$; 14, maxillary palpus, sensilla, and apical pit, $\times 6000$; 15, metasternum, discrimen and male setal tufts (arrows), $\times 130$; 16, plastron setae on elytron, $\times 600$.

rax and metathorax (Fig. 38). Legs short, 5 segmented. Spiracles peripneustic, functional; present on mesothorax and abdominal segments 1–8; spiracles on abdominal segment 8 on upper third. Abdominal segments 1–5 incomplete rings, parallel sided,

without pleura; each segment with narrow sternal groove. Abdominal segments 6–8 complete sclerotized rings. Abdominal segment 9 tapering to a rounded apex; with operculum. Anal gills and hooks absent.

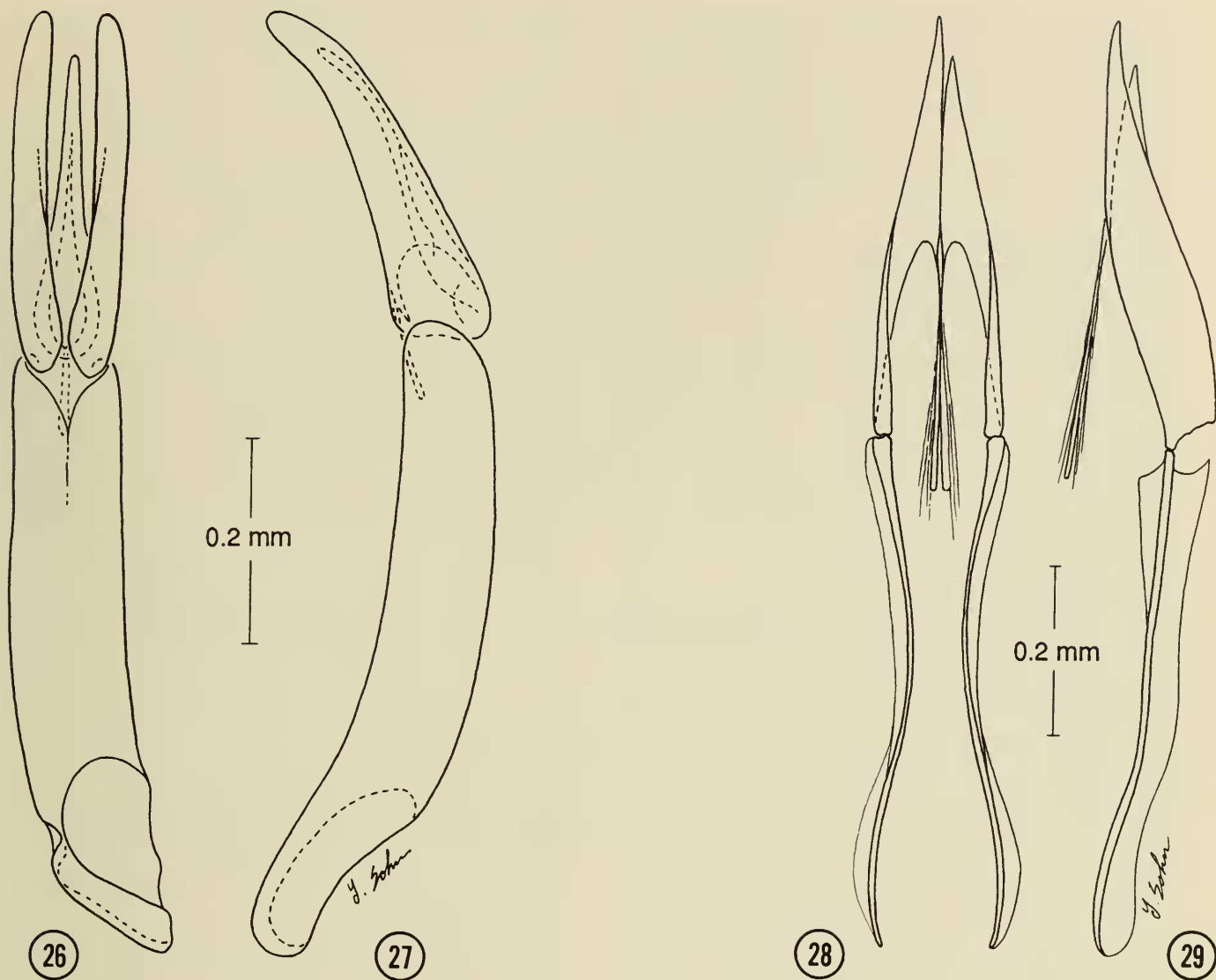
Comparative notes.—We consider *Sty-*



Figs. 17–25. *Stygoparnus comalensis*, new genus, new species: Figures 17–21, adult, male: 17, head, vestigial eye (arrow), and pronotum, $\times 80$; 18, head, vestigial eye (arrow), ventral view, $\times 130$; 19, head and vestigial eye (arrow), lateral view, $\times 270$; 20, metathoracic wings, vestigial, dorsal view, $\times 80$; 21, metathoracic wing, vestigial, lateral view, $\times 150$. Figures 22–25, larva: 22, head, adoral view, $\times 170$; 23, head, lateral view, $\times 170$; 24, antenna, $\times 1300$; 25, maxillary palpus, $\times 1400$.

goparnus to be related to *Helichus* (Figs. 41–46) and they share the following synapomorphies (adults, 1–4): (1) adults aquatic; (2) last abdominal sternum without setae; (3) ventral surface densely and conspicuously granulate; (4) ovipositor long, blade-like (Figs. 28, 29); (5) larva with operculum rounded apically (Fig. 40).

Although we believe *Stygoparnus* is closely related to *Helichus*, *Stygoparnus* exhibits the following apomorphic character states not present in members of *Helichus* (adults, 1–5): (1) eyes vestigial (Figs. 11, 17–19); (2) antennae, 8 segmented (Fig. 7); (3) metathoracic wings vestigial (Figs. 20, 21); (4) discrimen extended only half length of



Figs. 26–29. *Stygoparnus comalensis*, new genus, new species: 26, male genitalia, dorsal view; 27, male genitalia, lateral view; 28, ovipositor, dorsal view; 29, ovipositor, lateral view.

metasternum (Fig. 15); (5) elytra without striae (Figs. 6, 8); (6) larva with lateral spiracles on abdominal segment 8 on upper third of segment (Figs. 30, 39).

Stygoparnus comalensis, new species
Figs. 6–40

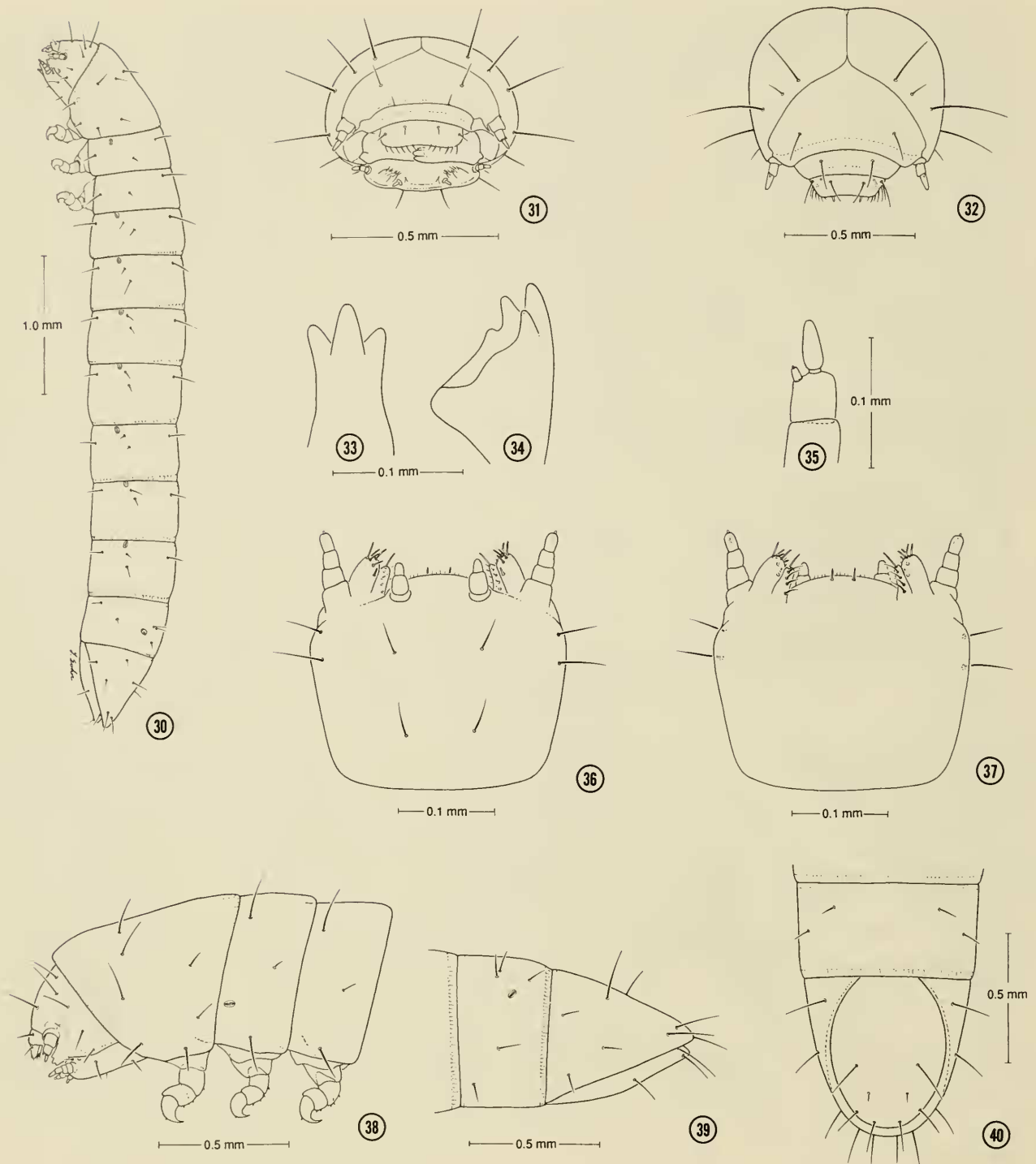
Holotype ♂. — Body form and size: Elongate, subparallel; depressed dorsally, convex ventrally. Length, 3.12 mm; width, 1.00 mm.

Color: Entirely reddish brown; cuticle thin and translucent.

Head: Moderately shining; finely punctate; punctures separated by 2 times di-

ameter of puncture; each puncture bearing a medium long, fine, white seta. Eyes vestigial, reduced to minute, subcircular, un-faceted, ocellus-like structures (Figs. 11, 17–19, arrows). Clypeus expanded laterally; rather bare and shining medially, with few punctures; punctures becoming more dense laterally. Labrum densely pubescent, shallowly emarginate apically; anterolateral angles rounded.

Thorax: Pronotum 0.88 mm long, 0.85 mm wide; widest medially; anterior margin subtruncate; posterior margin trisinate; anterolateral pronotal angles moderately acute (Fig. 17); posterolateral angles moderately acute; disc shining, with small punc-



Figs. 30–40. *Stygoparnus comalensis*, new genus, new species, larva: 30, habitus, lateral view; 31, head, adoral view; 32, head, frontal view; 33, mandible, ventral view; 34, mandible, lateral view; 35, antenna; 36, maxillolabial plate, ventral view; 37, maxillolabial plate, dorsal view; 38, head and thorax, lateral view; 39, abdominal segments 8 and 9, lateral view; 40, abdominal segments 8 and 9 and operculum, ventral view.

tures separated by about 5 times diameter of puncture; punctures adjacent to disc each bearing a fine white seta with apex directed toward meson; declivous margins covered by whitish plastron setae interspersed with elongate granules bearing fine, recumbent

setae; prescutellar emargination present. Scutellum large, suboval; appearing hollow because of more darkly sclerotized margin. Elytra 2.28 mm long, 1.00 mm wide; humeral angles obtuse, not prominent; apicolateral margins deeply grooved to receive

expanded lateral margins of last abdominal sternum; surface covered by whitish plastron setae interspersed with elongate granules bearing fine, recumbent setae (Fig. 16). Prosternum shining medially, with sparse setae and punctures; laterally with plastron setae and elongate granules bearing recumbent setae separated by 1 to 3 times granule width. Plastron setae especially evident on mesepisternum, mesepimeron, and metepisternum. Metasternum covered with plastron setae and elongate granules separated by 2 to 3 times granule width and each bearing a fine seta (Fig. 15). A tuft of fine, sparse, longer setae on each side of discrimen on metasternum (Fig. 15, arrows). Legs each with femur and tibia with fine setae and densely granulate. Femoral lengths: 0.75, 0.70, 0.87 mm. Tibial lengths: 0.88, 0.85 mm, 1.05 mm. Tibia with dense golden brown medial fringe of tomentum.

Abdomen: Sterna 1–4 with plastron setae interspersed with elongate granules separated by 2 to 3 times granule width and each bearing a fine seta. Apical sternum without plastron setae, shining; smooth basomedially, elsewhere punctures separated by puncture diameter and each bearing a fine seta; lateral margins moderately bent upward to clasp tips of elytra.

Genitalia: As illustrated (Figs. 26, 27).

Allotype.—Similar to male; length 3.12 mm, width 0.98 mm. Scutellum broader and more triangular. Metasternal tufts absent. Ovipositor as illustrated (Figs. 28, 29).

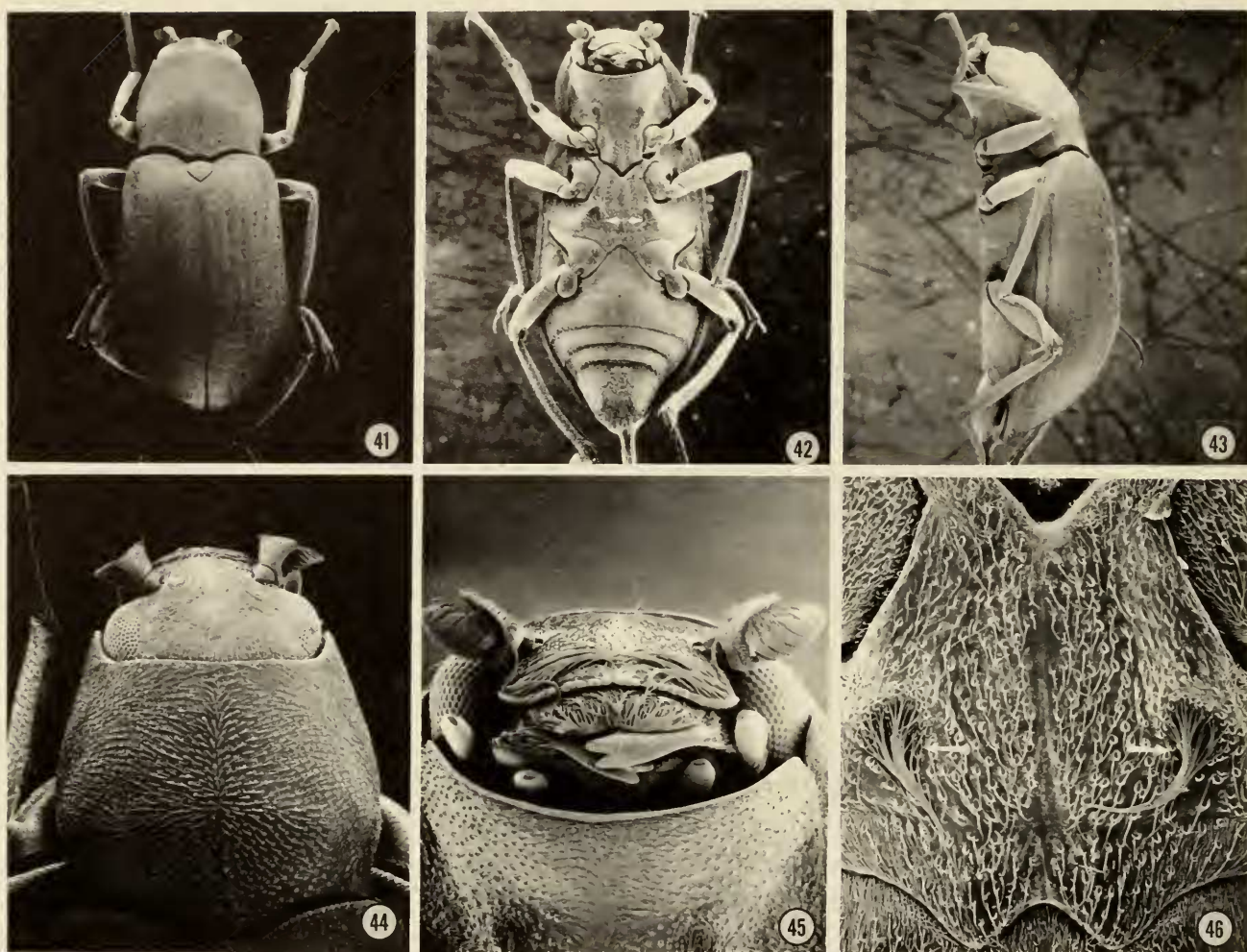
Variations.—Very little variation was noted among individuals. Males averaged slightly larger than females when measurements of 18 males and 13 females were compared: total length: ♂ 3.00–3.70 mm, ♀ 2.88–3.60 mm; width: ♂ 0.95–1.10 mm, ♀ 0.92–1.12 mm; pronotal length: ♂ 0.85–0.96 mm, ♀ 0.84–0.95 mm; pronotal width: ♂ 0.78–0.88 mm, ♀ 0.76–0.88 mm; elytral length: ♂ 2.08–2.40 mm, ♀ 2.00–2.40 mm.

Larva (late instar; by association).—Form and size: Cylindrical (Fig. 30). Length, 6–8 mm; width, 0.8–1.0 mm.

Color: Light yellow brown.

Head: Partially retracted into pronotum. Ovate in adoral and frontal view (Figs. 31, 32). Width about 1.2 times height; cranium with 5 setae in dorsoventral line on each half posteriad of epicranial suture; all setae curving laterally, 1 seta posteriad of and parallel to ventral seta. Gular suture indistinct. Frons with 2 setae positioned equally between meson and lateral margin; anteclypeal margin shallowly emarginate. Clypeus with width 4 times length; postclypeus sclerotized; anteclypeus membranous, with 4 setae. Antenna (Figs. 24, 31, 35) inserted anteriorly of mandibles, directed ventrally; segment 1 about 1.5 times as wide as segment 2; segment 2 about 2 times as wide as segment 3 and shorter than segments 1 or 3; sensillae on segment 1, intersegmental membrane between segments 2 and 3, and antennal appendix; antennal appendix about 0.3 times length of apical segment (Fig. 24). Mandibles tridentate (Figs. 33, 34), wedge shaped; length 1.3 times width; mesal surface slightly concave; middle tooth longest; basal pigmentation brown, apex black; molar process absent. Maxillolabium a rectangular plate; dorsal surface glabrous medially, with 2 setae on anteromedial margin (Fig. 37); ventral surface glabrous except with 8 setae—1 at each base of labial and maxillary palpi, 2 near posteromedial margin, and 2 on anterolateral margin near bases of maxillary palpi (Fig. 36). Maxillary palpus (Fig. 25), 4 segmented; tapering toward apex; segments subequal in length; 1 or more cone shaped sensillae on each segment. Galea and lacinia distinctly separate. Galea lobate, directed slightly mesad, with a row of 6 spines on dorsoapical surface. Lacinia digitate, directed mesad; with a row of 5 apicomedial spines on dorsal surface. Labial palpus, 3 segmented; segments unequal in length; apical segment with width about 0.5 times width of penultimate segment and 3 or 4 sensillae on anteromedial margin.

Thorax (Fig. 38): Pronotum, along dor-



Figs. 41–46. *Helichus suturalis* LeConte, male: 41, habitus, dorsal view, $\times 20$; 42, habitus, ventral view, $\times 20$; 43, habitus, lateral view, $\times 20$; 44, head, normal eyes, and pronotum, dorsal view, $\times 40$; 45, head and mouthparts, adoral view, $\times 80$; 46, metasternum, discrimen and male setal tufts (arrows), $\times 110$.

somedian line, longer than combined length of mesonotum and metanotum; conceals head to dorsal arm of epicranial suture; with transverse row of setae at about anterior third, setae arising closer to anterior margin ventrally. Mesonotum rugose anteriorly, becoming glabrous posteriorly. Mesothorax with ventral, anterolateral spiracle. Metathorax similar to mesothorax but lacking spiracle. Legs similar. Prothoracic pair large; coxa dome shaped, slightly wider than long; trochanter longer on posterior surface than on anterior surface; femur slightly longer and broader than tibiotarsus; tibiotarsus tapering apically; pretarsus sclerotized, pigmented apically; claw robust, curved.

Abdomen: Glabrous. Segments 1–9 with anterior dorsal margins without rows of ridges; intersegmental membranes striolate.

Sterna 1–5 narrow, folded, membranous or lightly sclerotized, fused with pleurites, forming incomplete rings, with narrow sternal groove. Terga 6–8 fused ventrally, forming rings. Segment 8 (Fig. 39) with dorsal surface slightly longer than ventral surface; lateral surface with 3 long setae above and 2 long setae below level of spiracle. Spiracles present on lower third of segments 1–7 (Fig. 30) and on upper third of segment 8 (Fig. 39). Segment 9 (Fig. 39) with 6 long lateral setae on each side; apex subacute in lateral view; dorsal surface striolate along anterior margin. Operculum covering cloacal chamber; with 4 long setae on posterior margin, 2 long setae slightly posteriad of midlength, and 2 short setae equidistant from meson and lateral margins (Fig. 40). Anal gills and abdominal hooks absent.

Type data.—Holotype ♂: United States: Texas: Comal County, New Braunfels, Landa Park, Comal Springs, Comal 2 spring-head/run, 2 May 1988, C. B. Barr; deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Allotype: Same data as the holotype.

Paratypes: Fifty-one adults and 6 larvae, all from same locality as holotype: 25 Apr 1987, H. P. Brown, 3 adults; 1 Aug 1987, C. B. Barr, 2 adults; 23 Apr 1988, H. P. Brown, 7 adults; 28 Apr 1988, C. B. Barr, 7 adults, 1 larva; 2 May 1988, C. B. Barr, 10 adults, 3 larvae; 6 Jun 1988, W. D. Shepard, 22 adults, 2 larvae. Paratypes will be deposited in the following collections: American Museum of Natural History, New York, New York; California Academy of Sciences, San Francisco, California; Canadian National Collection, Ottawa, Canada; Louisiana State University Insect Collection, Baton Rouge, Louisiana; Muséum National d'Histoire Naturelle, Paris, France; Natural History Museum, London, England; Oklahoma Museum of Natural History, Norman, Oklahoma; Texas Agriculture and Mechanical University, College Station, Texas; National Museum of Natural History, Smithsonian Institution, Washington, D.C.; and the private collections of C. B. Barr and W. D. Shepard.

Etymology.—Named for Comal Springs, Texas, the type locality.

Laboratory Observations

Ten live beetles were brought back to the laboratory to observe their behavior. They were kept in a glass bowl, 20 cm in diameter and 7 cm deep, on a substrate of small rocks taken from Comal Springs. Water filling the bowl also came from the springs; as it evaporated, it was replaced with distilled water. A small aquarium pump and bubblestone provided aeration.

Stygoparnus comalensis seems to be rather fragile as a result of being lightly sclerotized. Three beetles died within about 2 weeks, and only one survived longer than

four months. Most had visible trauma or damage of some type (i.e., missing tarsal claws, legs, or antennae; cuticle punctures; etc.). The single survivor lived for 21 months, and it appears that its death was caused by the sudden addition of large amounts of new water.

Although the beetles rested and crawled on all surfaces of the rocks, most of their time was spent on the sides or undersides. A couple of individuals spent a notable amount of time just below the air-water interface on rocks that projected out of the water. In one instance, a beetle was observed totally above water for a few minutes atop a wet rock. Beetles were often seen grazing on the rock surfaces. Small amounts of leaf litter taken from the springs were periodically added to the bowl, but the beetles were not observed feeding on the fragments.

The most interesting behavior, noted once, was what might have been a plastron grooming procedure. A beetle just below the surface lifted its head and pronotum through the film, and re-submerged with a bubble of air encasing the mouthparts and a separate bubble between the pronotum and elytra. It then made chewing-type motions, passed both middle legs into and through the bubbles, and rubbed the legs down the sides of the body; this act was repeated multiple times. This particular beetle had very sparse plastron setae. The development and extent of the area of plastron setae seemed to vary among individuals. The plastron setae probably had been abraded in some individuals.

Discussion

The discovery of a troglobitic dryopid raises many questions. Most puzzling is the fact that the subterranean habitat must be amenable to both the aquatic adults and the larvae that are believed to be terrestrial. Where is the population centered and what is its geographic extent? Why has a supposedly hypogean beetle been found in an epi-

gean habitat? Where do the larvae develop and pupate? Because we know little of the natural history of *Stygoparnus*, we can only hypothesize about the answers. Perhaps the population is concentrated in an underground cavern not far from where the springs issue, or maybe it dwells just below the surface because of the limitations of the immature stages. The occurrence of the beetles at the surface could be due to the amount of spring flow or availability of food resources. It has been hydrologically determined that the individual orifices at Comal Springs are fed by more than one flow path (Ogden et al., 1986). This may explain why the species has not been found in any of the other spring orifices, especially Comal 1 and 3 that are in close proximity (Fig. 1).

Acknowledgments

We are especially indebted to Harley P. Brown, University of Oklahoma, Norman, who first collected this species and directed the senior author to the type locality. David Whatley, Director of Parks and Recreation for the City of New Braunfels, Texas, is thanked for providing background information and granting permission to collect at Comal Springs in Landa Park. Dr. Glenn Longley, Director of the Edwards Aquifer Research and Data Center in San Marcos, Texas, was instrumental in providing resource information and data on the aquifer and associated springs.

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(CBB) Department of Entomology, Louisiana Agricultural Experiment Station,

Louisiana State University Agricultural Center, Baton Rouge, Louisiana 70803-1710, U.S.A. (current address: Department of Biological Sciences, California State University, Sacramento, California 95819, U.S.A.); (PJS) Department of Entomology, National Museum of Natural History, NHB-169, Smithsonian Institution, Washington, D.C. 20560, U.S.A.